

Cyphocarpus perennis (Asterales, Campanulaceae, Cyphocarpoideae), a new species endemic to the Andes of the Atacama Desert, Chile

Ludovica Santilli¹, Natali Cruz², Claire De Schrevel³, Philippe Dandois³, Nicolás Lavandero⁴,
Maria Fernanda Perez⁴

¹ Santiago, Chile

² Comunidad Indígena Colla Dos Álamos, Tierra Amarilla, Copiapó, Chile

³ Copiapó, Chile

⁴ Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Avenida Libertador B. O'Higgins 340, Santiago, Chile

Corresponding author: Nicolás Lavandero (nlavand@uc.cl)

Abstract

A new species, *Cyphocarpus perennis* **sp. nov.**, endemic to the Andes of the Atacama Desert of Chile is here described. Based on new nrDNA ITS sequence data, phylogenetic analyses place this novel species as sister to the remaining species of the genus. *Cyphocarpus perennis* presents unique characters within the genus, such as a perennial habit and a compact leafy rosette. A detailed description, distribution map, insights about its habitat, conservation status, photographs and an updated key to *Cyphocarpus* are provided. As for most species found in the Atacama Region, mining activities and climate change represent a major threat for its conservation.

Resumen

Se describe una nueva especie, *Cyphocarpus perennis* **sp. nov.**, endémica de los Andes del Desierto de Atacama de Chile. Con base en nuevos datos de secuencias de rDNA ITS, análisis filogenéticos sitúan la nueva especie como hermana del resto de las especies del género. *Cyphocarpus perennis* posee caracteres únicos dentro del género, tales como un hábito perenne y hojas organizadas en una roseta compacta. Se provee una descripción morfológica detallada, un mapa de distribución, información sobre el hábitat, estado de conservación, fotografías y una clave dicotómica actualizada para la identificación de las especies de *Cyphocarpus*. Como es el caso de varias especies altoandinas de la región de Atacama, las actividades mineras y el cambio climático representan las mayores amenazas a su conservación.

Key words: Andes, biodiversity, Cyphocarpoideae, phylogeny, taxonomy



Academic editor: Bin-Bin LIU

Received: 10 April 2025

Accepted: 18 May 2025

Published: 27 June 2025

Citation: Santilli L, Cruz N, De Schrevel C, Dandois P, Lavandero N, Perez MF (2025) *Cyphocarpus perennis* (Asterales, Campanulaceae, Cyphocarpoideae), a new species endemic to the Andes of the Atacama Desert, Chile. PhytoKeys 259: 111–129. <https://doi.org/10.3897/phytokeys.259.155414>

Copyright: © Ludovica Santilli et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Cyphocarpus Miers is a genus composed of three currently described species within the family Campanulaceae which are all endemic to northern Chile. The genus was first described by Miers (1848) based on specimens

collected by Thomas Bridges in the region of Coquimbo, near Paihuano (30°01'S 70°31'W). Miers recognized the uniqueness of its morphology and described the subfamily Cyphocarpoideae, placing the first described species, *Cyphocarpus rigescens* Miers, within the class Campanulaceae (sensu Jussieu 1789), based on the epigynous corolla and alternipetalous stamens. Sandwith (1931) described the second species of the genus, *Cyphocarpus innocuus* Sandwith, based on specimens collected by Elliot and Gourlay in 1927 in Andacollo valley, Coquimbo region (30°13' S 71°04' W), at approximately 1000 m above sea level (a.s.l.). The last species, *Cyphocarpus psammophilus* Ricardi, was described in 1959 based on specimens collected the same year in the locality of Cachiuyo, Huasco, Atacama region (29°02'S, 70°53'W) at approx. 800 m a.s.l.

The most comprehensive systematic work made of *Cyphocarpus* was done by Hansen (2016), who tested the historical hypotheses concerning the evolution of Campanulaceae and the placement of Cyphocarpoideae Miers using chloroplast genomes and the nuclear ribosomal cistron. The study included sampling of all five subfamilies and all three extant species of *Cyphocarpus*. According to Hansen (2016), the monogeneric subfamily Cyphocarpoideae is sister to Nemacladoideae, which, together with Lobelioideae, forms an early divergent lineage within Campanulaceae. The author suggests that the distribution of Cyphocarpoideae can be explained by a dispersal from either the Nearctic or Neotropics (Hansen 2016).

Regarding its morphology, alike all Campanulaceae, *Cyphocarpus* possesses latex-producing laticifers both in vegetative and floral organs (Lammers 1992). It also has zygomorphic, bilabiate corollas, similar to Lobelioideae, Cyphioideae, and some Nemacladoideae. However, unlike the aforementioned clades, in Cyphocarpoideae, the upper lip is composed of a single corolla lobe that forms a hood whose margins are connivent so that it remains tightly closed. The margin is winged at the distal end of the hood, the wings fuse and form an appendage that projects off the hood (Hansen 2016). Another distinctive character of the genus is the presence of three prominent yellow ridges at the palate which are the result of induplicate estivation of the corolla lobes.

According to the protologues, field and herbarium observations, all *Cyphocarpus* species are annual herbs and to date they are considered to be endemic to Chile. This is not surprising as Chile is known to harbour one of the 35 world biodiversity hotspots, given its high number of endemic species and high levels of threat (Myers et al. 2000; Mittermeier et al. 2004). This hotspot called “Chilean winter rainfall-Valdivian forests”, is mostly located in central Chile with its northern distribution placed in the Atacama region (Arroyo et al. 2004). The climate in the region is marked by low precipitation during the winter, low relative humidity inland, and strong daily variation in temperature.

The issues with conservation are particularly critical for central Chile and the “Norte Chico”, with less than 5% of the territory under protection and the pressure of human activity such as overgrazing, burning, land clearance for agriculture and mining activities (Squeo et al. 2001; Arroyo et al. 2006; Armesto et al. 2007). Moreover, climate change predictions estimate an increase of up to 5 °C in temperature in the high elevations of the Andes and a decrease in precipitations by 2065 (Juliá et al. 2008) which may affect the vegetation of these elevations.

Thus, it is of fundamental importance to systematically describe new species unknown to science, as conservation efforts cannot be effective without an exhaustive inventory and a deep understanding of the biodiversity that composes the ecosystems we aim to protect.

The aim of the present study is to describe a new species of *Cyphocarpus* from the Andes of the Atacama Desert, in northern Chile, study its phylogenetic position, describe its distribution and habitat, providing a preliminary conservation assessment according to the IUCN criteria, as well as a dichotomous key of the genus.

Methods

Herbarium studies and fieldwork

During the austral summer of 2024, several botanical expeditions were made near to the locality of Morros Negros, Tierra Amarilla district, Atacama Region, Chile. Specimens that could not be assigned to any known species were found. Recordings of observations of the habitat were made in the field along with collection of herbarium material, pickled specimens in ethanol 70%, preservation of leaf tissues for molecular analyses in silica gel and measurements of plant size. All collections were obtained with the permission of the Comunidad Indígena Dos Álamos, the Colla indigenous community who owns the land where the putative new species was collected. All specimens collected during fieldwork were deposited in SGO and CONC (acronyms following Thiers 2025). Besides the revision of the herbaria material (CONC, ULS, SGO), a thorough search was performed on iNaturalist (<https://www.inaturalist.org/>) in order to find possible observations that matched the morphology of the new species.

Localities

The locality of collection of the type specimen is situated at approximately 19 km southeast of Juntas del Potro, in the district of Tierra Amarilla, located in the central east of the Atacama region, nearly 100 km from Copiapó and 120 km from Vallenar at ca. 3637 m a.s.l. (Fig. 1). To characterise the area, we consulted the bioclimatic and vegetation classification of Chile by Luebert and Plis-coff (2017). According to this classification, the locality corresponds to a low tropical-mediterranean Andean shrub dominated by *Adesmia hystrix* Phil. and *Ephedra breana* Phil. Additionally, we reviewed iNaturalist observations, which, although not based on collected specimens, provide georeferenced data useful for expanding knowledge of the species' distribution. The localities from iNaturalist, whose specimens have not been collected yet, are both found in the district of Tierra Amarilla, specifically at approximately 24 km south of Iglesia Col-orada, along route C-463 (<https://www.inaturalist.org/observations/50569276>), and approximately 17 km south of Carrizalillo along route C-503 (<https://www.inaturalist.org/observations/50569279>). Both localities belong to the low tropical-desertic Andean shrub dominated by *Atriplex imbricata* D.Dietr. The Atacama Region is found between latitudes 26°–29° S, the climate is characterized by low precipitation concentrated in a limited period of time during the winter season, a strong decrease in relative humidity inland, and a considerable daily variation in the atmospheric temperature (Juliá et al. 2008).

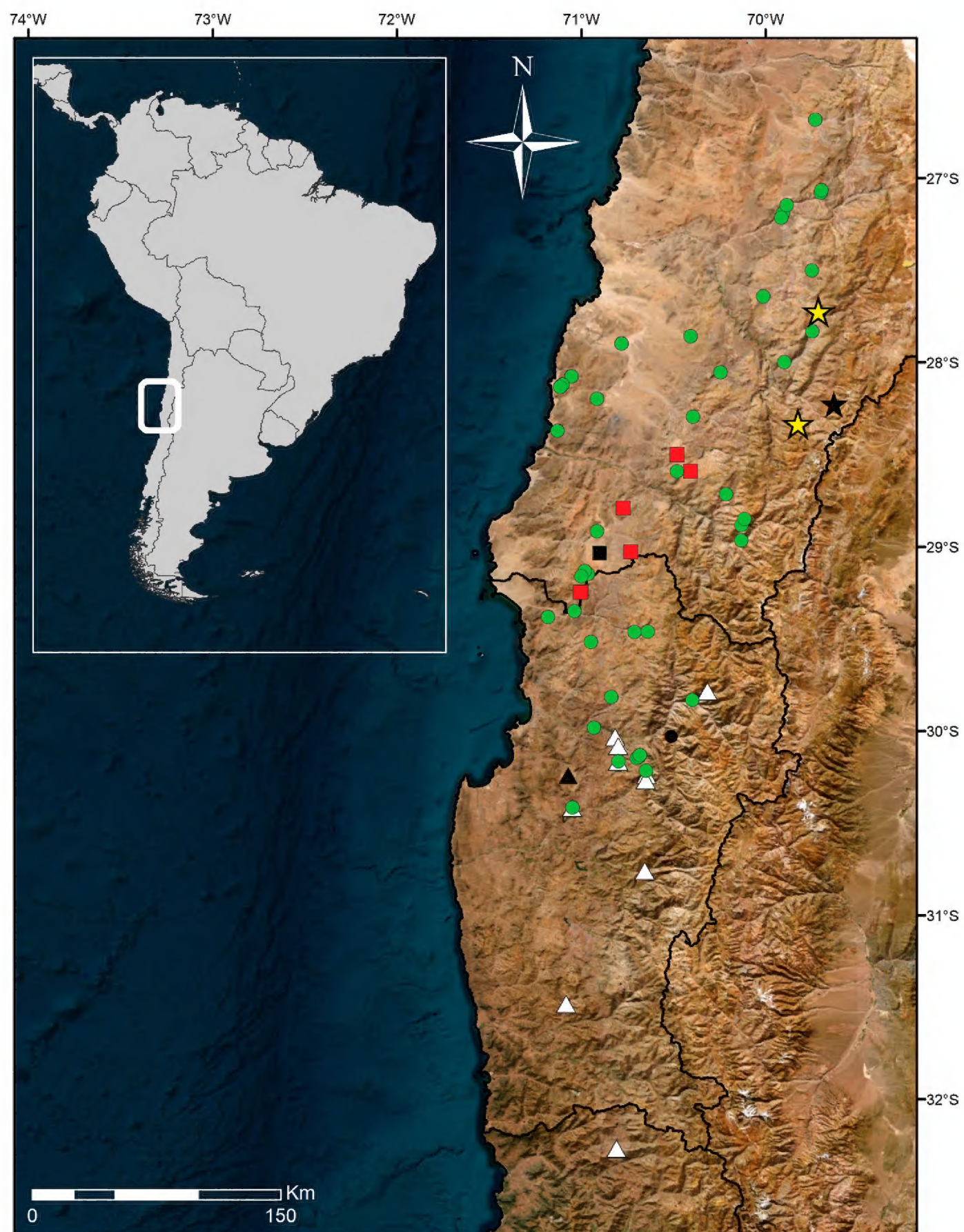


Figure 1. Distribution map of *Cyphocarpus*. Green circles: *C. rigescens*; white triangles: *C. innocuus*; red squares: *C. psammophilus*; yellow stars: *C. perennis*. Type localities for each species are shown in black. Black line indicates boundaries between administrative regions of Chile and the borderline between Chile and Argentina. Service Layer Credits: Esri Maxar Earthstar Geographics and the GIS user community.

Morphological analysis

Morphological analyses were based on both fresh and dried specimens collected by the authors during field trips in December 2024. Photographs of living plants were taken in the field. To accurately describe the species, plants were dissected and observed under a stereoscope. Terminology for describing plant morphology follows Beentje (2016) and Hansen (2016). All measurements were performed using an analog caliper, and both minimum and maximum values for each character were recorded to capture the full range of variation. The selected traits were chosen based on their relevance to species identification and differentiation within the genus *Cyphocarpus*. These characters are commonly used in taxonomic studies to distinguish species and are consistent with previous morphological analyses in related taxa.

Conservation status

The preliminary assessment of the conservation status of the species was made using the International Union for Conservation of Nature (IUCN 2012) categories and criteria, following the most recent guidelines (IUCN Standards and Petitions Committee 2024). The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCat (Bachman et al. 2011).

DNA extraction, amplification, sequencing, and phylogenetic analyses

Total genomic DNA from the holotype of the new species (*CDS-931*, SGO) was extracted from silica-dried material using the Qiagen DNeasy Plant Mini Kit (QIAGEN) following the manufacturer's instructions. Genomic DNA was used to amplify by PCR a partial region of the nuclear ribosomal DNA (nrDNA), comprising a region of the 18S rRNA gene, the internal transcribed spacer 1 (ITS1), the 5.8S rRNA gene, the internal transcribed spacer 2 (ITS2) and a partial region of the 26S rRNA gene. Amplification was performed using the primers ITS4 and ITS5 (White et al. 1990). The PCR thermocycling conditions consisted of 95° C for 5 min of initial denaturation, followed by 30 cycles of 95° C for 1 min, 55° C for 1 min, and 72° C for 1.5 min, and a final extension step of 72° C for 15 min. We amplified this region in 25 µL PCR reactions using 12.5 µL GoTaq® G2 Green Master Mix (PROMEGA), 1 µL of each primer (10 µM), 1.25 µL BSA, 6.75 µL nuclease-free water, and 2.5 µL of DNA (~100 ng/µL). Sanger sequencing was performed using the same primers for amplification. Sequencing was performed in the Plataforma de Secuenciación y Tecnologías Ómicas, Pontificia Universidad Católica de Chile, using the ABI PRISM 3500 xl Genetic Analyzer (Applied Biosystems™). Forward and reverse sequences were assembled using Geneious Prime 2022.2.1 (<https://www.geneious.com>). As a preliminary analysis, we BLASTed (<https://blast.ncbi.nlm.nih.gov/>) the assembled sequence, obtaining the highest match to *Cyphocarpus rigescens* (90.85%). Having confirmed its affinity to *Cyphocarpus*, we extracted and amplified with the aforementioned methods one specimen from the three other species of the genus (*C. rigescens*, *C. innocuus* and *C. psammophilus*). GenBank accession numbers for all newly generated DNA sequences and voucher information are given in Suppl. material 1.

Phylogenetic analyses included a sampling of the closest genera of *Cyphocarpus*, according to Hansen (2016). These include *Nemacladus* and *Pseudonemacladus*, from the Nemacladoideae subfamily. As an outgroup, we used *Codonopsis pilosula* (Campanuloideae). A broader sampling within Campanulaceae could not be performed due to the high degree of divergence of the ITS sequences, which complicated the assessment of homology in the alignment. The assembled sequences generated by this study and the sequences downloaded from Genbank (<https://www.ncbi.nlm.nih.gov/genbank/>) were aligned using the MAFFT v.7.490 (Katoh et al. 2002; Katoh and Standley 2013) algorithm in Geneious Prime 2022.2.1 (<https://www.geneious.com>). Phylogenetic analyses were performed for both Maximum-likelihood (Felsenstein 1981), using RAXML-SSE3 version (Stamatakis 2014) included in RAXMLGUI v.2.0.10 (Edler et al. 2021) and Bayesian inference using MrBayes x64 v3.2.7 (Ronquist et al. 2012), respectively. The gaps and indels were treated as missing data. The GTR+I+G model of nucleotide sequence evolution was determined based

on the Akaike information criterion (AIC) given by MrModeltest v2 (Nylander 2004). Maximum likelihood analyses were run using the GTRGAMMA approximation, which approximates to a GTR model. The analysis included 1000 ML slow bootstrap replicates with 500 runs. Bayesian analyses were conducted under the GTR+I+G model, with two independent runs for 1 million generations, sampling every 1000 generations. Time series plots and effective sample size (ESS) were analysed using TRACER v.1.7 (Rambaut et al. 2018) to check convergence for each run. The first 250.000 generations were discarded as burn-in.

Results

The ITS nucleotide matrix, representing a total of 4 ingroup and 6 outgroup accessions, contained 701 characters. The alignment contained 416 (59.3%) identical sites and 115 parsimony-informative sites. The topology of both Bayesian and Maximum likelihood analyses yielded congruent topologies (Fig. 2), recovering a strongly supported monophyletic *Cyphocarpoideae* (PP = 1, BS = 85) as sister to monophyletic *Nemacladoideae* (PP = 0.99, BS = 0.87), also with strong support. Within *Cyphocarpoideae*, the new species, *Cyphocarpus perennis*, appears as sister to the rest of *Cyphocarpus* (PP = 0.99, BS = 83). *Cyphocarpus psammophilus* appears as sister to the clade formed by *Cyphocarpus innocuus* and *Cyphocarpus rigescens*, although the latter clade has low support (PP = 0.57, BS = 50). These results confirm the phylogenetic affinity of this new species to the genus *Cyphocarpus*.

Taxonomic treatment

Cyphocarpus perennis Santilli & Lavandero, sp. nov.

[urn:lsid:ipni.org:names:77364408-1](https://nomenclature.ipni.org/names/77364408-1)

Figs 3–5

Type. CHILE • Atacama: Copiapó, Tierra Amarilla, Cerro Morros Negros, 28°13'42"S, 69°37'48"W, 3,613 m, 27 December 2024, fl., *Claire de Schrevel, Natali Cruz & Philippe Dandois* CDS-931, (holotype SGO 171975!; isotype CONC).

Diagnosis. *Cyphocarpus perennis* differs to other *Cyphocarpus* species due to its perennial habit, rosette-like growth form, rounded leaves, and tomentose indumentum.

Description. Perennial herb, forming groups of seasonally persistent annual rosettes, up to 3 cm tall and 4 cm wide. **Rhizome** creeping to extended, lignified and branching, buried several centimetres below the substrate. **Stems** emerging from the nodes of the rhizome, almost entirely subterranean, belowground portion up to 15 cm long, glabrous, bearing leaves reduced to scales, aerial portion of the stem pubescent (same indumentum of the leaves), up to 3 cm long. **Leaves** flabellate, densely strigose to hirsute, trichomes subulate, petioles up to 5 times as long as the lamina, approx. 15 mm long, arranged in short internodes. **Lamina** as long as wide, up to 6 mm long and 6 mm wide, crisped; base attenuate towards the petiole; apex rounded; margin crisped, bidentate. **Inflorescence** an axillary solitary flower, subtended by small leaflike bracts. **Flowers** pentamorous, sessile, epigynous, zygomorphic, bilabiate, hermaphrodite, protandrous. **Sepals** 5, free, linear, $\frac{1}{5}$ of corolla tube length, same indumentum as leaves,

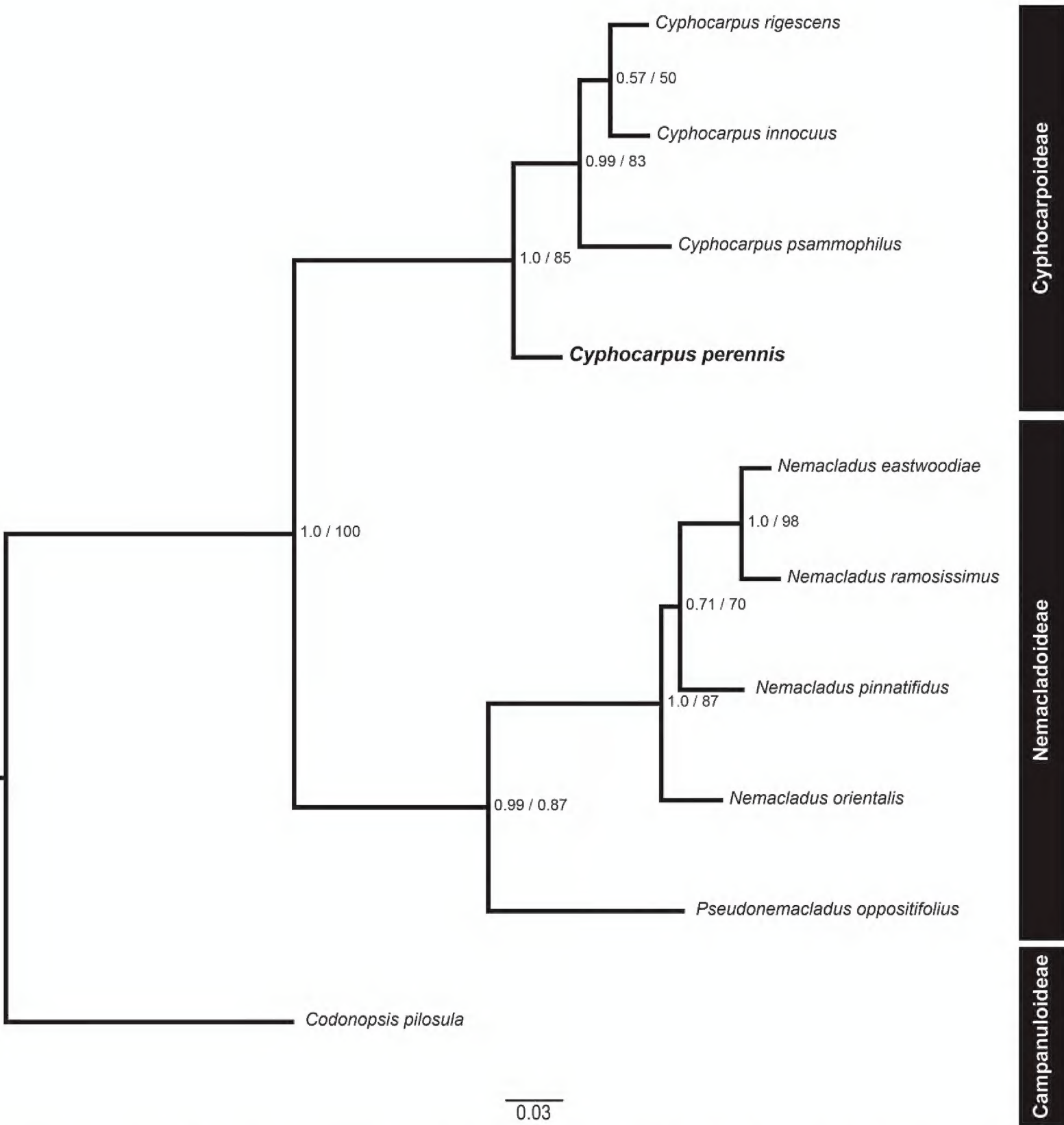


Figure 2. Phylogeny of *Cyphocarpus* resulting from Bayesian analysis of the ITS region. Branch lengths indicate substitutions/site. Numbers next to the nodes represent the posterior probabilities from the Bayesian analysis and bootstrap values from the Maximum Likelihood analysis (PP/BS). The new species *Cyphocarpus perennis* is shown in bold.

margin entire. **Petals** 5, hirsute outside, glabrous inside, basally fused into a 13–15 mm long corolla tube, then free; lobes white, the upper lip comprised of a single corolla lobe, ca. 4 mm long, that forms a hood with connivent, winged margins; wings fused at the distal end of the hood to form a small appendage that slightly projects off the hood; the remaining 4 ventral corolla lobes, ca. 5 mm long, forming a palate ca. 11 mm wide, with three prominent yellow ridges at the base, alternating with the lobes. **Stamens** 5, epipetalous, haplostemonous, free portion of the filaments ca. 3 mm, pubescent, anthers included in corolla tube, connivent around the style, longitudinally dehiscent. **Ovary** inferior, hirsute, cylindrical, syncarpous; carpels 2, locules 1, placentation parietal, style 1, 16–17 mm, stigma globose, 1 × 2 mm, slightly two-lobed, included in the hood and eventually protruding from it. **Fruit** a rounded capsule, 10–11 × 10 mm, hirsute, crowned by persistent sepals, becoming papery and releasing the seeds by irregular longitudinal ruptures. **Seeds** ca. 2 mm long, cylindrical and slightly curved, pale yellow to brown, surface ribbed longitudinally.

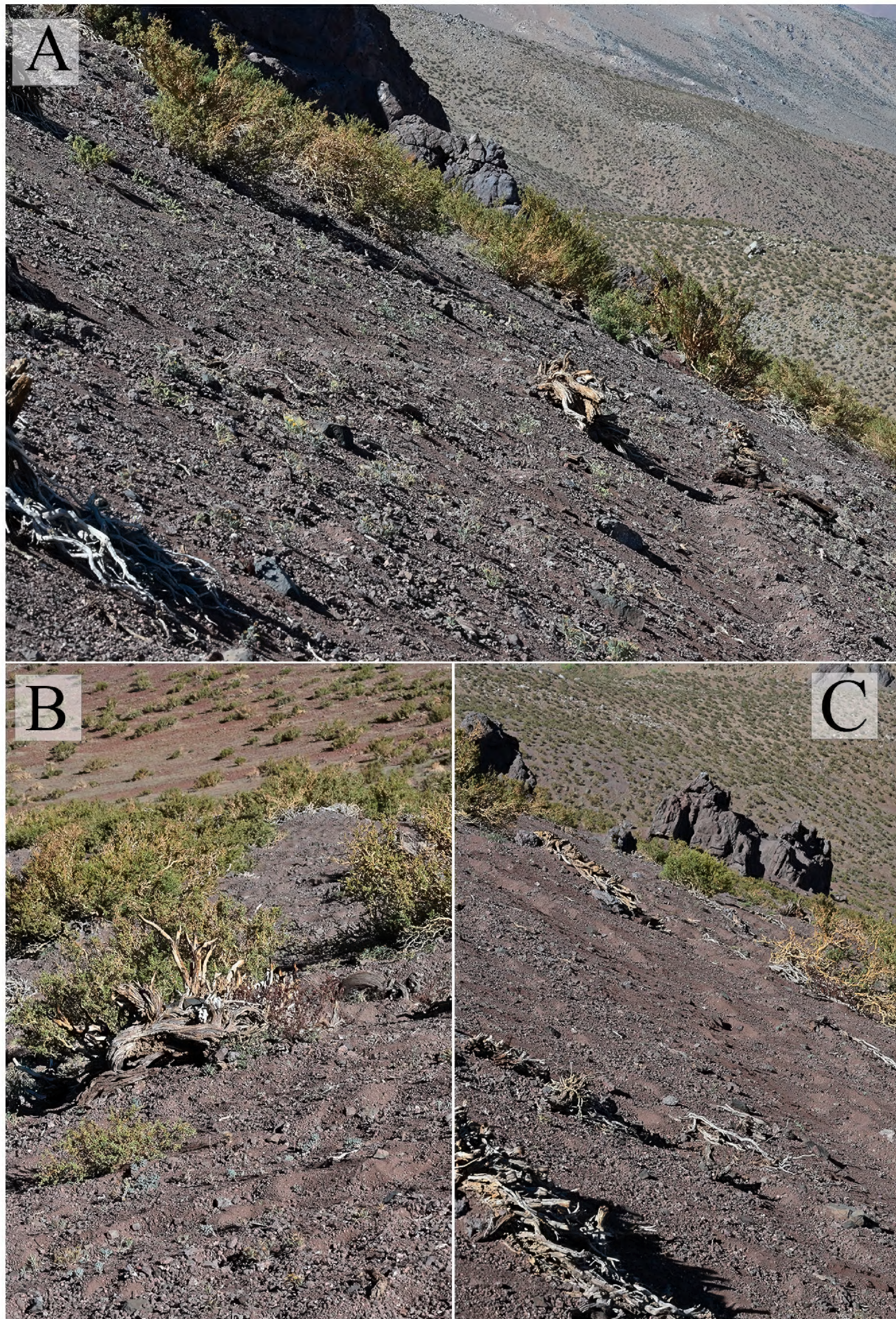


Figure 3. *Cyphocarpus perennis*. **A–C.** Habitat of *Cyphocarpus perennis* showing gravelly slopes dominated by *Adesmia hystrix*.

Etymology. The specific epithet refers to the perennial habit which distinguishes the novel species from the other species of the genus, which are all annual herbs.

Phenology. Flowering from late November to early January.

Distribution and habitat. Endemic to the eastern Andean ranges of the Atacama Desert, in the municipality of Tierra Amarilla. It is known from the localities of Morros Negros, Carrizalillo and Iglesia Colorada (Fig. 1). The species is recorded to grow at high elevations between approx. 2900 and 3700 m, in loose gravelly and sandy soil, at full sun exposure.

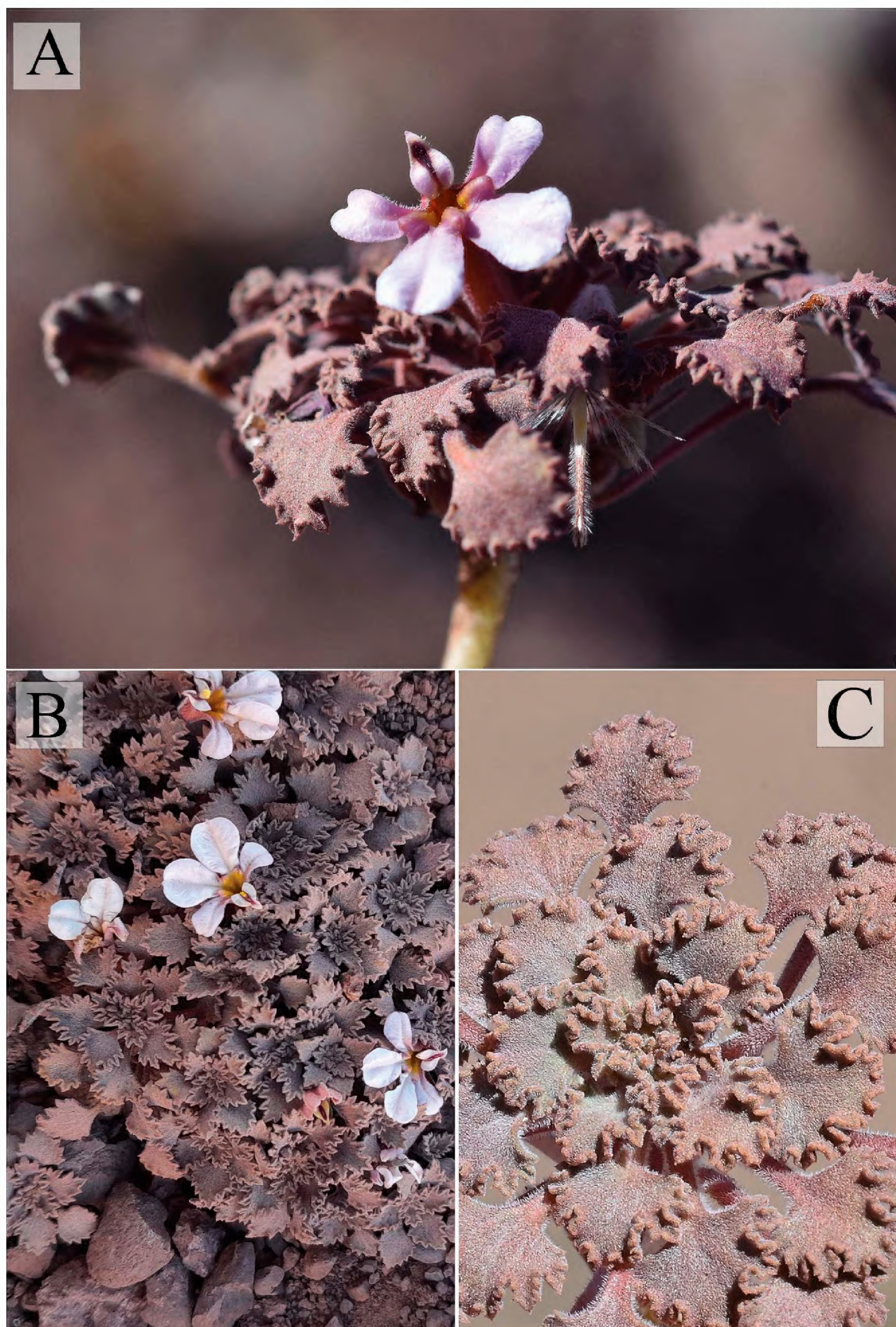


Figure 4. *Cyphocarpus perennis*. **A.** General view of the plant; **B.** Upper view of the plant; **C.** Details of the vegetative rosette.

Associated vegetation. *Cyphocarpus perennis* has been observed at elevations near the upper limit of the arborescent growth, represented by a scrub of *Adesmia hystrix* Phil. Accompanying species recorded in the field include *Adesmia hystrix*, *Menonvillea cuneata* (Gillies & Hook.) Rollins, *Doniophyton weddellii* Katinas & Stuessy, *Pachylaena atriplicifolia* D. Don ex Hook. & Arn.

Conservation status. *Cyphocarpus perennis* is assessed here as Endangered (EN) under the IUCN categories and criteria B1ab(iii) + 2ab(iii). Criteria B1 and B2 were selected because its extent of occurrence (EOO) is < 5,000 km²

(588.908 km²) and its area of occupancy (AOO) is < 500 km² (12 km²). Criterion “a” was selected because it is known to exist in only three locations, criterion “b(iii)” was selected because there is a projected decline in the area, extent, and quality of habitat. According to Luebert and Pliscoff (2017), the low tropical-desertic Andean scrub is not represented in the national system of protected area and its extent is projected to decrease by 48.45% under the IPCC AR5 scenario 2.6, and by 63.37% under the scenario 8.5 for the period 2040–2070. Similarly, the low tropical-mediterranean Andean scrub dominated by *Adesmia hystrix* and *Ephedra breana* is expected to decrease its extent by 27.21% under the IPCC AR5 scenario 2.6 and by 30.05% under the scenario 8.5 for the period 2040–2070. Additionally, high Andean plants are particularly sensitive to global warming and the reduction in snow cover and precipitation is worsened by the increase of temperatures which are predicted to keep rising by models of climate change (Juliá et al. 2008; Cordero et al. 2019). Moreover, *Cyphocarpus perennis* is found in the second region with more mining concessions in Chile (after Antofagasta), with more than 8,918 concessions and nearly 2,500,000 ha under this real estate right (SERNAGEOMIN 2024). All localities where the species is found are under mining concessions (<https://catastro.sernageomin.cl/>). Finally, *Cyphocarpus perennis* is not present in any statal or private protected area in Chile. It is important to highlight that the type locality of the species is within the boundaries of the indigenous Colla community of Dos Álamos, and permission must be requested to enter.

Additional material examined. CHILE • Atacama Region: [Copiapó Province] Cerro Morros Negros 28°13'37"S, 69°37'45"W, 3637 m, 27 Dec 2024, *Claire de Schrevel, Natali Cruz & Philippe Dandois* CDS-929 (SGO!); • Cerro Morros Negros 28°13'38"S, 69°37'45"W, 3636 m, 27 Dec 2024, *Claire de Schrevel, Natali Cruz & Philippe Dandois* CDS-930 (SGO!); • Cerro Morros Negros 28°13'42"S, 69°37'48"W, 3613 m, 27 Dec 2024, *Claire de Schrevel, Natali Cruz & Philippe Dandois* CDS-932 (SGO!); • 24 km south of Iglesia Colorada, along route C-463, 27°43'22"S, 69°42'47"W, 9 Jan 2018, observation by Aira Francisca Faúndez Fallau (<https://www.inaturalist.org/observations/50569276>); • Approx. 17 km south of Carrizalillo along route C-503, 28°19'55"S, 69°49'31"W, 10 Jan 2018, observation by Aira Francisca Faúndez Fallau (<https://www.inaturalist.org/observations/50569279>).

***Cyphocarpus innocuus*: CHILE • Coquimbo Region: [Choapa Province]** Reserva Nacional Las Chinchillas, Qda. Los Pilques, 31°28'60"S, 71°04'60"W, 1100 m, 01 Oct 2002, *L. Suarez* 1115 (CONC); • **[Elqui Province]** Los Algarrobos, Km. 40–41 Vicuña-Hurtado, 30°16'00"S, 70°39'00"W, 1200 m, 29 Nov 1939, *R. Wagenknecht* 18445 (CONC); • Andacolla [Andacollo] Valley, 30°14'30"S, 71°04'16"W, 900 m, Oct 1927, *C. Elliott & W. Balfour Gourlay* 98 (K); • Cerro Tololo, 30°10'00"S, 70°47'60"W, 1800 m, 07 Nov 2008, *M. Rosas* 6033 (CONC); • Quebrada San Carlos, 30°04'60"S, 70°47'60"W, 700 m, Dec 1974, *Edding & Villagrán* s.n. (CONC); • Quebrada San Carlos, 30°01'60"S, 70°49'00"W, 520 m, 05 Oct 1991, *G. Arancio* 91623 (ULS); • 15 Km. Al interior de Guanta, 29°46'60"S, 70°19'00"W, 1850 m, 06 Dec 1991, *G. Arancio* 91948 (ULS); Cuesta de Andacollo, 16 Sept 1957, *C. Muñoz* 4280 (SGO); • **[Limarí Province]** Los Molles, 30°45'32"S, 70°39'23"W, 1207 m, 15 Nov 1996, *L. Olivares* s.n. (ULS); • Corral Quemado, 30°25'00"S, 71°02'60"W, 1100 m, 30 Oct 1956, *C. Jiles* 3092 (CONC); • 6 Km North of Hurtado, 4 Km S of Portezuelo tres cruces, 30°14'17"S, 70°38'47"W, 1800 m, 31 Oct 1997, *T. Ayers et al.* 1514 (SGO); • **Valparaíso Region: [Petorca Province]** Cuesta de Alicahue,

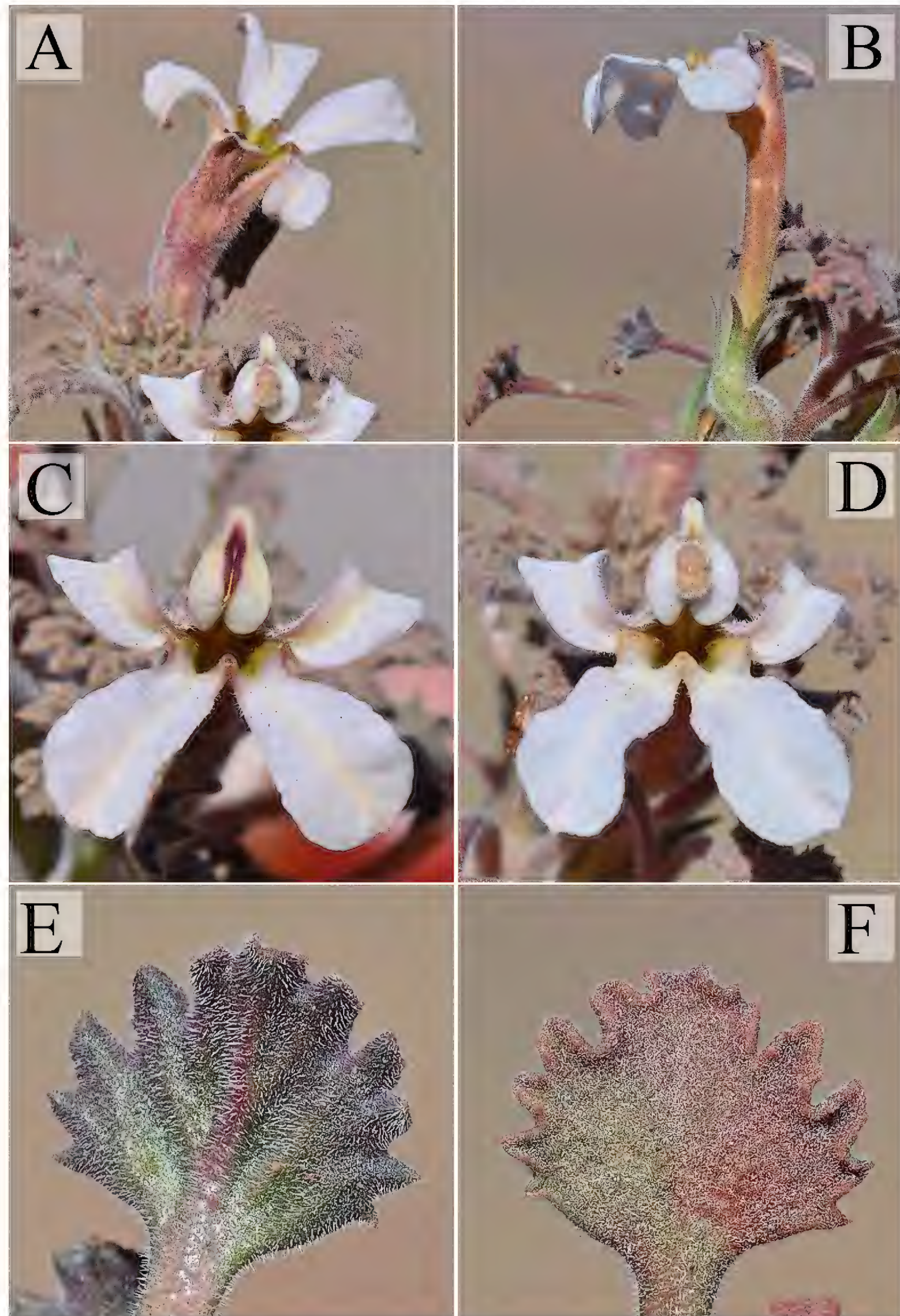


Figure 5. *Cyphocarpus perennis*. **A.** Upper view of a flower; **B.** Lateral view of a flower showing corolla tube and calyx; **C.** Frontal view of a flower during the male phase of the protandry; **D.** Frontal view of a flower during the female phase of the protandry; **E.** abaxial side of a leaf; **F.** adaxial side of a leaf.

32°16'19"S, 70°48'38"W, 1220 m, 06 Nov 2017, J. Macaya & al. 367 (CONC); Cuesta Alicahue, 32°16'01"S, 70°48'31"W, 1100 m, 09 Nov 1970, JP. Simon 112 (SGO).

***Cyphocarpus psammophilus*: CHILE • Atacama Region: [Huasco Province]**
Cruce a observatorio La Silla, 29°14'45"S, 71°00'19"W, 999 m, 08 Oct 1991,

G. Arancio 91604 (ULS); • Cruce a observatorio La Silla, 29°14'39"S, 71°00'02"W, 980 m, 08 Oct 1991, *G. Arancio* 91609 (ULS); • Peaje Cachiyuyo al Este, 29°04'60"S, 70°54'00"W, 370 m, 30 Oct 1991, *G. Arancio* 91753 (ULS); • Panamericana, Cruce a Observatorio La Silla, 29°04'60"S, 70°54'00"W, 370 m, 23 Sept 1991, *G. Arancio* 91658 (CONC); • 1 Km S de Cachiyuyo, 29°02'37"S, 70°54'16"W, 950 m, 22 Oct 1971, *Marticorena & al.* 1766 (CONC); • Cachiyuyo, 29°01'60"S, 70°54'00"W, 23 Oct 1965, *F. Behn s.n.* (CONC); • Cachiyuyo, 29°01'60"S, 70°54'00"W, 800 m, 19 Oct 1957, *Ricardi & Marticorena* 4460 (CONC); • Camino a los observatorios La Silla y Campana, 29°01'44"S, 70°43'57"W, 1641 m, 23 Sept 1991, *G. Arancio* 91650 (ULS); • Agua Amarga, 27.1 Km S of junction to Vallenar, 1.5 Km E of Hwy 5, 28°47'23"S, 70°46'19"W, 1050 m, 02 Nov 1997, *T. Ayers et al.* 1553 (SGO); • C-455 Los Morteros, 28°35'24"S, 70°24'25"W, 2062 m, 18 Nov 2022, *C. De Schrevel* 577 (CONC); • C-455 Los Morteros, 28°35'24"S, 70°24'25"W, 2062 m, 18 Nov 2022, *C. De Schrevel* 578 (CONC); • Huasco. Qda. San Antonio, 28°29'59"S, 70°28'53"W, 1717 m, 14 Dec 2011, *M. Rosas* 7869 (ULS).

***Cyphocarpus rigescens*: CHILE • Atacama Region: [Chañaral Province]** Ruta C-257 al Oeste, 26°40'60"S, 69°43'60"W, 1845 m, 25 May 2007, *L. Letelier & J. Reyes* 1360 (ULS); • **[Copiapó Province]** Quebrada Yervas Buenas, 28°03'19"S, 70°14'48"W, 1200 m, 12 Oct 2010, *M. Rosas* 6988 (ULS); • Valle del [Río] Jorquera, 28°00'00"S, 69°54'00"W, 12 Jan 1979, *Gunckel* 4056 (CONC); • Quebrada de Totoral (Boquerones), 27°53'60"S, 70°46'60"W, 160–180 m, 24 Nov 1941, *E. Pisano & R. Bravo* 793 (CONC, SGO); • Cerro Bandurrias, 27°51'33"S, 70°24'32"W, Dec 1888, *Geisse* 9569 (CONC); • Valle del Río Jorquera, 27°49'60"S, 69°45'00"W, 12 Jan 1970, *O. Zöllner* 4056 (CONC); • Camino a Lomas Bayas, 27°38'36"S, 70°00'56"W, 1385 m, 18 Oct 2022, *C. de Schrevel* 428 (CONC); • Quebrada San Miguel, km 46, 27°30'10"S, 69°45'06"W, 2021 m, 19 Apr 2006, *M. Rosas* 3690 (ULS); • Camino Tinogasta, Quebrada Cruz de Cañas, 27°13'00"S, 69°55'00"W, 1100 m, 06 Jan 1973, *Marticorena & al.* 473 (CONC); • Hwy 31, 54–56 Km NE of Copiapó, 27°11'25"S, 69°54'28"W, 1165 m, 05 Nov 1997, *T. Ayers et al.* 1581 (SGO); • Camino al Salar de Maricunga Km. 56, 27°04'44"S, 69°42'10"W, 1780 m, 31 Jan 1963, *Ricardi & al.* 541 (CONC); Quebrada de San Andrés, 27°04'00"S, 69°42'00"W, 1000 m, 03 Nov 1963, *F. Behn s.n.* (CONC); • Quebrada de Puquios, 1885, *Geisse* (SGO); **[Huasco Province]** Inicio norte Cuesta Pajonales, Km 580, 29°09'49"S, 71°00'03"W, 1015 m, 28 Oct 2002, *M. Muñoz* 4250 (SGO); • Cuesta Pajonales, 29°08'60"S, 70°58'00"W, 900 m, 16 Sept 1957, *Ricardi & Marticorena* 4382/767 (CONC); • Cuesta Pajonales, 29°07'60"S, 70°58'60"W, 1150 m, 31 Oct 1991, *R. Rodríguez* 2763 (CONC); • Cajon del Río Conay, 3 Km al interior de Conay, 28°58'00"S, 70°07'60"W, 1450 m, 13 Oct 1983, *Marticorena* 9558 (CONC); • 1.5 Km al E de Conay, 28°55'00"S, 70°55'00"W, 2000 m, 12 Dec 2008, *M. Rosas* 6159 (CONC); • Rio Laguna Grande, entre las Papas y Potrero de Toledo, 28°52'60"S, 70°07'60"W, 2000–2400 m, 19 Jan 1983, *Marticorena & al.* 83344 (CONC); • Rio Laguna Grande, Entre la Junta de Valeriano y Las Papas, 28°51'00"S, 70°07'00"W, 1800–2000 m, 18 Jan 1983, *Marticorena & al.* 83313 (CONC); • R.N.P. Los Huascoaltinos, Qda. Seca, 28°42'59"S, 70°13'00"W, 2067 m, 12 Dec 2008, *Y. Tracol & M. Leon* 6278-12 (ULS); • Cuesta Los Morteros, Pre-cordillera, 28°35'33"S, 70°28'57"W, 1940 m, 16 Oct 2011, *Mieres s.n.* (CONC); • Quebrada Baratillo Sur, 28°22'17"S, 71°07'51"W, 55 m, 06 Oct 2017, *C. Delpiano* 520 (ULS); • Quebrada Las Máquinas C-461, 28°17'48"S, 70°23'47"W, 954 m,

25 Oct 2022, *C. de Schrevel* 464 (CONC); • Sector Higuera Norte, 28°11'53"S, 70°55'02"W, 418 m, 10 Nov 2008, *A. Stoll & J. Nickerl* 1519 (ULS); • Camino a Carrizal Bajo, 28°07'60"S, 71°07'00"W, 250 m, 31 Oct 1991, *G. Arancio* 91685 (CONC, ULS); • Camino Canto del Agua, Cerca de Carrizal Bajo, 28°07'17"S, 71°06'11"W, 83 m, 27 Sept 2016, *P. Medina* 3142 (CONC); • Camino Totoral a carrizal, 28°04'37"S, 71°03'15"W, 585 m, 28 Oct 1989, *J. Armesto* 89734 (ULS); • Cordón Aguadita, Cerro El Volcán, 10 May 1998, *L. Minoletti s.n.* (SGO); • **Coquimbo Region: [Elqui Province]** Rio Seco, Los Choros, Tres Cruces, 30°13'00"S, 70°39'00"W, 700 m, 21 Sept 1975, *O. Zöllner* 8333 (CONC); • Cerro Tololo, 30°10'00"S, 70°47'60"W, 1800 m, 26 Nov 1967, *C. Jiles* 5126 (CONC); Camino a Hurtado, 30°08'60"S, 70°42'00"W, 1410 m, 23 Oct 2008, *M. Rosas* 5895 (ULS); • Camino Río Hurtado-Vicuña, bajando hacia Vicuña, 30°08'32"S, 70°41'27"W, 1460 m, 11 Nov 2017, *J. Macaya & al.* 412 (CONC); • 16 Km. N of Portezuelo tres cruces, 30 Km N of Hurtado, 12–14 Km S of Vicuña, 30°08'28"S, 70°41'22"W, 1400 m, 01 Nov 1997, *T. Ayers et al.* 1543 (SGO); • 10 Km al sur de Vicuña, en el camino a Hurtado, 30°07'60"S, 70°40'60"W, 800–1000 m, 13 Oct 1940, *G. Looser* 4284 (CONC); • Camino Vicuña-Hurtado, Cuesta el Almendro, 30°07'60"S, 70°40'60"W, 1150 m, 10 Oct 1939, *R. Wagenknecht* 18452 (CONC); • Sides of Mountains near Payguano [Paihuano], 30°01'47"S, 70°30'48"W, 1841, *Bridges* 1298 (E); El Molle, 29°58'60"S, 70°55'60"W, 600 m, Nov 1952, *C. Jiles* 2347 (CONC); • Quebrada Guanta, 29°49'60"S, 70°24'00"W, 1300 m, 06 Nov 1991, *G. Arancio* 91818 (ULS); Cuesta de la viñita, al interior de Marquesa. Camino al Mineral de Arqueros, 29°48'59"S, 70°50'19"W, 20 Sept 1957, *C. Muñoz* 4205 (SGO); • Mineral Los Plomos, 16 Km al S de Tres Cruces, 29°31'05"S, 70°56'59"W, 900–1200 m, 03 Nov 1949, *W. Biese* 2908 (SGO); • Ruta D-115, 29°27'50"S, 70°42'50"W, 1340 m, 26 Jan 2009, *A. Stoll & G. Arancio* 1970 (ULS); • Los Corrales al N, 29°27'45"S, 70°38'29"W, 2028 m, 26 Jan 2009, *A. Stoll & G. Arancio* 1983 (ULS); • Cerca Mineral Los Fierros, 29°22'60"S, 71°10'60"W, 540 m, 31 Oct 1961, *R. Wagenknecht* 908 (CONC); • 104 Km S of Vallenar, near turnoff to Punta Colorada, 29°21'03"S, 71°02'21"W, 430 m, 01 Dec 1991, *U. Eggli & B.E. Luenberger* 1839 (SGO); Rio Turbio, *Volckmann s.n.* (SGO); • **[Limarí Province]** Corral Quemado, 30°25'00"S, 71°02'60"W, 1100 m, 05 Oct 1950, *C. Jiles* 3501 (CONC).

Key to the species of *Cyphocarpus* (Fig. 6)

- 1 Perennial herb; stems compressed so leaves appear to be arranged in a compact rosette; petioles longer than lamina, lamina as long as wide, margins undulate with mucronate teeth (Fig. 6C) ***C. perennis***
- Annual herbs; stems more or less elongated, never forming a compact rosette; petioles as long or shorter than lamina, lamina at least twice as long as wide, margins not undulate **2**
- 2 Glandular indumentum; floral bracts 1–2 mm long, filiform, entire; wings of the upper lobe not elongated (Fig. 6B) ***C. psammophilus***
- Scabrid to pilose indumentum; floral bracts 20–30 mm long, toothed; wings of the upper lobe notably elongated **3**
- 3 Calyx margin serrate (Fig. 6D) ***C. rigescens***
- Calyx margin entire (Fig. 6A) ***C. innocuus***

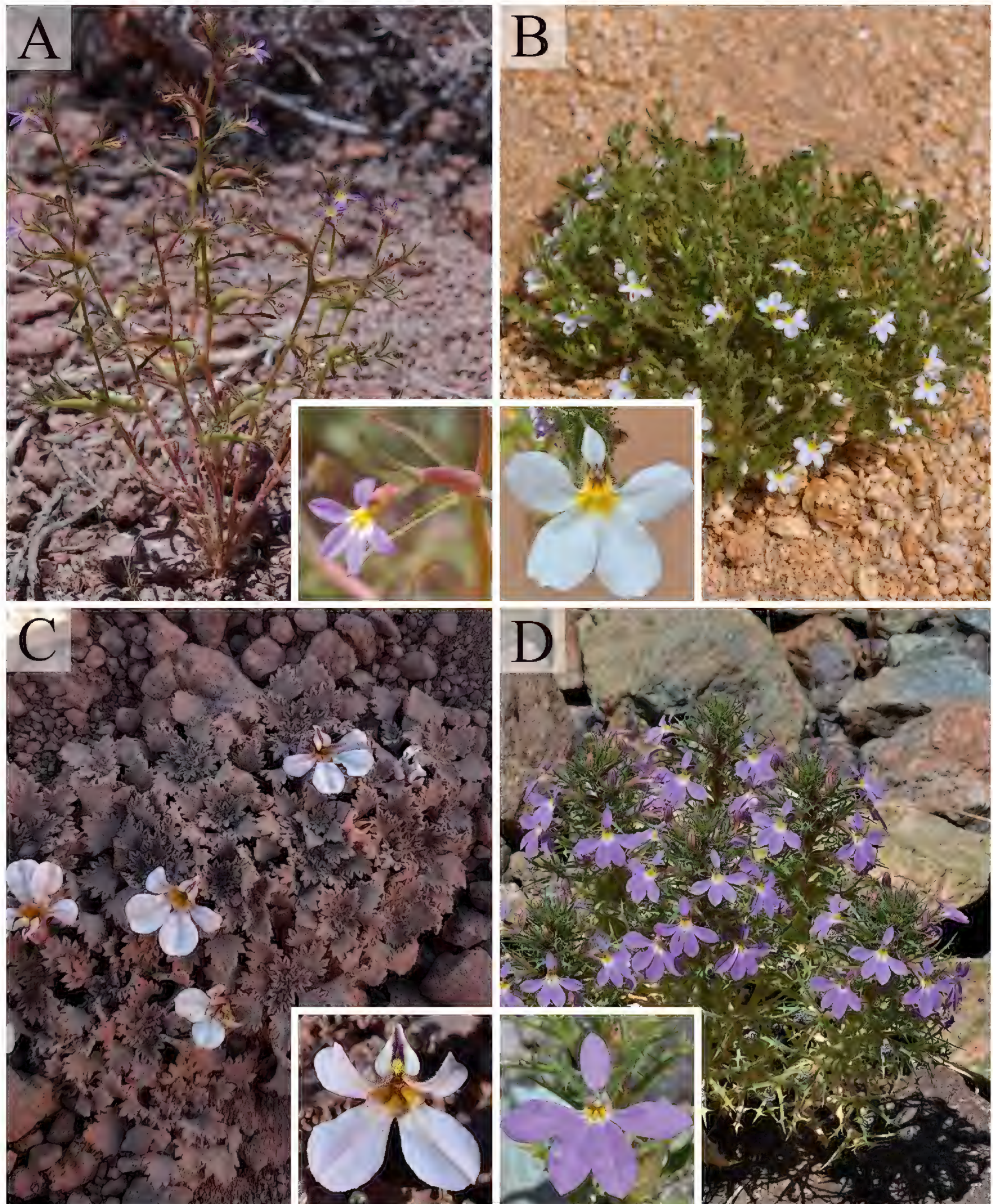


Figure 6. Comparative plate of *Cyphocarpus* species. **A.** *C. innocuus* habit and detail of flower (Marcelo Rosas); **B.** *C. psammophilus* habit (Marcelo Rosas) and detail of flower (Claire de Schrevel); **C.** *C. perennis* habit (Natali Cruz) and detail of flower (Claire de Schrevel); **D.** *C. rigescens* habit and detail of flower (Claire de Schrevel).

Discussion

Our study confirms the endemism of *Cyphocarpus* to Chile, restricted to the Valparaíso, Coquimbo, and Atacama regions. However, the new species, *Cyphocarpus perennis*, extends the elevational distribution of the genus by about 1,300 meters, reaching up to 3,700 m. This increase in elevation coincides with a shift in life history strategy, as *Cyphocarpus perennis* is perennial

unlike the other three annual species in the genus (Lammers 2007). Several plant groups in the Andes present this pattern, such as *Adesmia* (Pérez et al. 2024), *Lupinus* (Hughes and Eastwood 2006), *Leucheria* (Pérez et al. 2020), among others (Hughes and Atchison 2015), where shifts from annual to perennial life forms are correlated with shifts from lowland to montane habitats. The shift to perennial habit is likely an adaptation to the harsh environmental conditions at high elevations, characterized by short growing seasons, frequent frosts, and high climate variability, which reduce the probability of completing the life cycle within a single year (Friedman 2020, Hughes and Atchison 2015, Bliss 1971). Likewise, several comparative studies have shown that perennial life cycles tend to shift to annual life histories in hot and dry conditions (Friedman 2020, Friedman and Rubin 2015).

Our phylogenetic results are consistent with those obtained by Hansen (2016). The topology of both Bayesian and Maximum Likelihood analyses of the nuclear DNA obtained by Hansen (2016) shows Cyphocarpoideae as sister to Nemacladoideae. Within Cyphocarpoideae, our topology is also consistent with both nuclear and plastid topologies obtained by Hansen (2016), showing *Cyphocarpus innocuus* as sister to *Cyphocarpus rigescens*, and this clade as sister to *Cyphocarpus psammophilus*. The placement of *Cyphocarpus perennis* within the genus *Cyphocarpus* was initially suggested based on its floral morphology, despite its unusual vegetative morphology. Interestingly, our results position *Cyphocarpus perennis* as sister to all other *Cyphocarpus* species. While our phylogenetic analyses were based solely on nuclear ribosomal DNA sequences, it is acknowledged that the incorporation of plastid or genome-wide data could potentially alter the phylogenetic placement of *Cyphocarpus perennis*. Such data would provide a more comprehensive understanding of its evolutionary relationships and address concerns related to incomplete lineage sorting or hybridization events. Therefore, future studies should consider a multilocus phylogenetic approach to further elucidate the phylogenetic placement and evolutionary history of *Cyphocarpus*.

Cyphocarpus perennis is not included in any protected area in Chile. The area where the species thrives is well known for its mining activities, focused mainly in copper and gold. The Atacama Region is one of the most exploited regions of Chile, with approximately 84% of its surface occupied by mining concessions, the highest among Chilean administrative regions (Ministerio de Minería 2022).

The discovery of *Cyphocarpus perennis*, a new endemic of the Andes of the Atacama Desert of Chile, highlights the exceptional biodiversity and high levels of endemism in this region. It also emphasises the need to increase fieldwork in the area. The Atacama Region is a hotspot of endemism, harbouring nearly 56% of Chile's endemic vascular plant species, with almost 8% restricted solely to this region (Squeo et al. 2008). Notably, in the past decade, nearly 25% of all newly described Chilean species are known to be found in the Atacama Region, surpassing any other region in the country (<https://www.ipni.org/>). It is likely that many more undescribed species remain to be discovered within this region. However, several challenges hinder comprehensive biodiversity research in the Atacama region. The steep topography, combined with the unpredictable annual variation in precipitation, severely limits accessibility and complicates fieldwork planning. Furthermore, the lack of accessible roads and the prevalence of privately owned land and restricted access due to mining activities pose substantial logistical and legal obstacles to field research efforts.

Acknowledgements

The authors would like to thank the curators of SGO, CONC, and ULS for their support with the herbarium material. We would also like to thank Ricardo Segovia and Juan Manuel Saez from the Biodata Program (Instituto de Ecología y Biodiversidad) for sharing digital images from herbarium specimens hosted at CONC and ULS. We thank Marcelo Rosas for sharing photographs of *Cyphocarpus innocuus* and *C. psammophilus*. We are also grateful to Ricardo Soto and Constanza Sánchez for their valuable assistance. We thank Martin Gardner, Nicolás García, and one anonymous reviewer for their helpful comments on the submitted manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was funded by the Agencia Nacional de Investigación y Desarrollo (ANID) Fondecyt-Chile grant 1252165 to Fernanda Pérez and Subdirección de Capital Humano/Doctorado Nacional/2023-21230402 to Nicolás Lavandero.

Author contributions

All authors have contributed equally.

Author ORCIDs

Ludovica Santilli  <https://orcid.org/0000-0001-5429-3441>

Philippe Dandois  <https://orcid.org/0000-0003-1955-1294>

Nicolás Lavandero  <https://orcid.org/0000-0002-2390-5078>

Maria Fernanda Perez  <https://orcid.org/0000-0001-5730-9760>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

- Armesto JJ, Arroyo MTK, Hinojosa LF (2007) The Mediterranean environment of central Chile. In: Veblen TT, Young KR, Orme AR (Eds) The physical geography of South America. Oxford University Press, New York, 184–199. <https://doi.org/10.1093/oso/9780195313413.003.0019>
- Arroyo MTK, Marquet P, Marticorena C, Simonetti J, Cavieres L, Squeo F, Rozzi R (2004) Chilean winter rainfall-Valdivian forests. In: Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da Fonseca GAB (Eds) Hotspots Revisited: Earth's Biologically Wealthiest and Most Threatened Ecosystems. CEMEX México, 99–103.

- Arroyo MTK, Marquet P, Marticorena C, Simonetti J, Cavieres L, Squeo F (2006) El hotspot chileno prioridad mundial para la conservación. Diversidad de Ecosistemas Terrestres. In: CONAMA (2008) (Ed.) Diversidad de Chile: Patrimonios y Desafíos. Ocho Libros, Santiago de Chile, 94–97. <https://repositorio.uchile.cl/handle/2250/120068>
- Bachman S, Moat J, Hill AW, De La Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. In: Smith V, Penev L (Eds) e-Infrastructures for data publishing in biodiversity science. ZooKeys 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Beentje H (2016) The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms (2nd edn). Royal Botanic Gardens Kew Press, 1–184.
- Bliss LC (1971) Arctic and alpine plant life cycles. Annual Review of Ecology, Evolution, and Systematics 2: 405–438. <https://doi.org/10.1146/annurev.es.02.110171.002201>
- Cordero RR, Asencio V, Feron S, Damiani A, Llanillo PJ, Sepulveda E, Jorquera J, Carrasco J, Casassa G (2019) Dry-Season Snow cover Losses in the Andes (18–40 S) driven by changes in Large-Scale climate Modes. Scientific Reports 9: 1–10. <https://doi.org/10.1038/s41598-019-53486-7>
- Edler D, Klein J, Antonelli A, Silvestro D (2021) raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. Methods in Ecology and Evolution 12(2): 1–5. <https://doi.org/10.1111/2041-210X.13512>
- Felsenstein J (1981) Evolutionary trees from DNA sequences: A maximum likelihood approach. Journal of Molecular Evolution 17: 368–376. <https://doi.org/10.1007/BF01734359>
- Friedman J, Rubin MJ (2015) All in good time: understanding annual and perennial strategies in plants. American Journal of Botany 102(4): 497–499. <https://doi.org/10.3732/ajb.1500062>
- Friedman J (2020) The evolution of annual and perennial plant life histories: Ecological correlates and genetic mechanisms. Annual Review of Ecology, Evolution, and Systematics 51(1): 461–481. <https://doi.org/10.1146/annurev-ecolsys-110218-024638>
- Hansen KM (2016) Phylogeny biogeography floral morphology of Cyphocarpoideae (Campanulaceae). Master's thesis, Northern Arizona University, 1–75. <https://openknowledge.nau.edu/id/eprint/2948/>
- Hughes CE, Atchison GW (2015) The ubiquity of alpine plant radiations: From the Andes to the Hengduan Mountains. The New Phytologist 207(2): 275–282. <https://doi.org/10.1111/nph.13230>
- Hughes C, Eastwood R (2006) Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. Proceedings of the National Academy of Sciences of the United States of America 103(27): 10334–10339. <https://doi.org/10.1073/pnas.0601928103>
- IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland Switzerland and Cambridge UK, iv + 32 pp. <https://portals.iucn.org/library/sites/library/files/documents/RL-2001-001-2nd.pdf>
- IUCN Standards and Petitions Committee (2024) Guidelines for Using the IUCN Red List Categories and Criteria. Version 16. Prepared by the Standards and Petitions Committee. <https://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Juliá C, Montecinos S, Maldonado A (2008) Características Climáticas de la Región de Atacama. In: Squeo F, Arancio G, Gutiérrez JR (Eds) Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Atacama. Ediciones Universidad de La Serena, 25–42. http://www.biouls.cl/lrojo/lrojo03/public_html/libro/flora_amenazada_atacama_03.pdf

- Jussieu AL (1789) Antonii Laurentii de Jussieu Genera plantarum: secundum ordines naturales disposita juxta methodum in Horto regio parisiensi exaratam. Parisiis, 163–166. <https://doi.org/10.5962/bhl.title.284>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Katoh K, Misawa K, Kuma KI, Miyata T (2002) MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Lammers TG (1992) Circumscription and phylogeny of the Campanulales. *Annals of the Missouri Botanical Garden* 79(2): 388–413. <https://doi.org/10.2307/2399776>
- Lammers TG (2007) Campanulaceae. In: Kadereit JW, Jeffrey C (Eds) *Flowering Plants Eudicots. The Families and Genera of Vascular Plants*. Springer, Berlin/Heidelberg, 8: 26–56. https://doi.org/10.1007/978-3-540-31051-8_5
- Luebert F, Pliscoff P (2017) Sinopsis bioclimática y vegetal de Chile. 2ª edición. Editorial Universitaria. Santiago, Chile, 381 pp. <https://repositorio.uchile.cl/handle/2250/181641>
- Miers J (1848) *Cyphocarpus*. In: Hooker WJ (Eds) *The London Journal of Botany: containing figures and descriptions of such plants as recommend themselves by their novelty, rarity, history, or uses; together with botanical notices and information, and occasional memoirs of eminent botanists (Vol.7)*. Hippolyte Baillière, Paris, 59–64. <https://www.biodiversitylibrary.org/item/6318#page/65/mode/1up>
- Ministerio de Minería de Chile (2022) Concesiones Mineras en Chile. Registro Propiedad Intelectual N° 2022-A-279. <https://www.minmineria.gob.cl/media/2022/01/MinMin-eri%CC%81a-2022-Concesiones-Mineras.pdf>
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da Fonseca GAB (2004) Hotspots revisited: Earth's biologically richest and most threatened ecoregions. CEMEX, Mexico City.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. <https://doi.org/10.1038/35002501>
- Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre Uppsala University.
- Pérez F, Lavandero N, Ossa CG, Hinojosa LF, Jara-Arancio P, Arroyo MTK (2020) Divergence in Plant Traits and Increased Modularity Underlie Repeated Transitions Between Low and High Elevations in the Andean Genus *Leucheria*. *Frontiers in Plant Science* 11: 714. <https://doi.org/10.3389/fpls.2020.00714>
- Pérez F, Lavandero N, Hinojosa LF, Cisternas M, Araneda D, Pinilla N, Moraga V (2024) Speciation and evolution of growth form in *Adesmia* DC (Dalbergieae, Fabaceae): The relevance of Andean uplift and aridification. *Frontiers in Plant Science* 15: 1403273. <https://doi.org/10.3389/fpls.2024.1403273>
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67(5): 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology* 61(3): 539–643. <https://doi.org/10.1093/sysbio/sys029>

- Sandwith N (1931) Decades Kewenses. Plantarum Novarum in Herbario Horti Regii Conservatarum. Decas CXXVI. Bulletin of Miscellaneous Information. Royal Botanic Gardens Kew 2: 96–105. <https://doi.org/10.2307/4102519>
- SERNAGEOMIN [Servicio Nacional de Geología y Minería] (2024) Anuario de la Minería de Chile 2023. Servicio Nacional de Geología y Minería Santiago, 198–202. <https://repositorio.sernageomin.cl/handle/0104/26211>
- Squeo FA, Arancio G, Gutiérrez JR (2001) Libro Rojo de los Sitios Prioritarios para su Conservación: Región de Coquimbo. Ediciones Universidad de La Serena, La Serena, Chile 3–11. <https://bibliotecadigital.ciren.cl/items/de22edd9-da46-4234-bb56-6565ba18a57a>
- Squeo FA, Arancio G, Letelier L, Marticorena A, Muñoz-Schick M, León-Lobos P, Arroyo MTK (2008) Estado de conservación de la Flora nativa de la región de Atacama. In: Squeo FA, Arancio G, Gutiérrez JR (Eds) Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Atacama. Ediciones Universidad de La Serena, La Serena, Chile, 45–49. http://www.observatoriocaldera.cl/biblioteca/589/articles-64766_documento.pdf
- Stamatakis A (2014) Raxml version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Thiers BM (2025) [continuously updated] Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/> [accessed 2025]
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: a guide to method and applications. Academic Press San Diego, 315–322. <https://doi.org/10.1016/b978-0-12-372180-8.50042-1>

Supplementary material 1

GenBank accession numbers for the ITS sequences used in this study

Authors: Ludovica Santilli, Natali Cruz, Claire De Schrevel, Philippe Dandois, Nicolás Lavandero, Maria Fernanda Perez

Data type: docx

Explanation note: GenBank accessions in bold are new to this study.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.259.155414.suppl1>